

A NEW PELOBATINE FROG FROM THE LOWER MIOCENE OF SOUTH DAKOTA WITH A DISCUSSION OF THE EVOLUTION OF THE *SCAPHIOPUS-SPEA* COMPLEX

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ABSTRACT: A new species of pelobatid frog, *Scaphiopus neuter*, is described from the Lower Miocene of the Wounded Knee area of South Dakota. The new species is a member of the Pelobatinae and it appears to lie within the genus *Scaphiopus*. Many of the characteristics of the fossil suggest that it is near the point of divergence of the subgenera *Scaphiopus* and *Spea*. Skeletal variation in Recent species of *Pelobates* and *Scaphiopus* is described as it relates to the taxonomic assignment of the fossil.

The taxonomic status of the North American pelobatine frogs, *Scaphiopus* Holbrook (1836) and *Spea* Cope (1866), has been debated for many years. The two groups of species are variously treated in the literature (usually without comment) as a single genus, or as separate genera or subgenera; see Zweifel (1956: 22) for a brief summary. The absence of related fossils from the early Cenozoic, the rarity of specimens from the middle Cenozoic (Oligocene-Miocene), Auffenberg (1956), and the fragmentary nature of the known fossil material from the late Cenozoic (Pliocene-Pleistocene), Bayrock (1964), Brattstrom (1964), Estes and Tihen (1964), Gehlbach (1965), Gut and Ray (1963), Holman (1958, 1959a, 1959b), Lynch (1965), Mecham (1959), Taylor (1936, 1938, 1941, 1942), Tihen (1954, 1960), and Zweifel (1956), has hindered the interpretation of the phylogenetic history of these taxa. I believe that the recent discovery of a fossil from the Lower Miocene, described herein, is a significant step toward elucidating the primary dichotomy in the complex. Because of the apparent intermediate phylogenetic position of the specimen between the two groups of previously recognized species it is referred to as

***Scaphiopus neuter*, new species**

Figures 1 through 6

Holotype: LACM 9209, collected by Harley J. Garbani on June 25, 1964; nearly complete skeleton with the exception of the distal parts of the limbs.

Type locality: LACM 1982 (= South Dakota School of Mines V5360; see Macdonald, 1963); in the gullies on both sides of the Sharps Cutoff road in the N. ½ of sect. 17, T. 39 N., R. 43 W, Wounded Knee area, Shannon County, South Dakota.

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Horizon: Approximately 225 feet above the base of the Sharps Formation, Arikaree Group, Lower Miocene (see Macdonald, 1963, for complete stratigraphic analysis).

Diagnosis: *Scaphiopus neuter* differs from all fossil and Recent species of the Pelobatinae in the following combination of characteristics: (1) nine free presacral vertebrae, (2) quadratojugal absent, (3) sternum cartilaginous (?), (4) transverse processes of vertebrae five through nine do not appear to project



Figure 1. Stereophotograph. Dorsal view of the holotype of *Scaphiopus neuter*. Actual size.

strongly anteriorly (the ninth vertebra may be exceptional), (5) coccyx fused to sacrum, (6) maxilla and squamosal not in contact, widely separated, (7) operculum large, (8) frontoparietal, squamosals, maxillae and nasals covered with slight to moderate amounts of encrusting dermal bone, (9) moderately large frontoparietal fontanelle present, inner borders of which are highly emarginate, (10) prootic foramen completely enclosed by bone, (11) palatine absent, (12) pterygoid process of maxilla absent, (13) dorsal protuberance of ilium very large, (14) postsacral webbing very extensive, and (15) two postsacral coccygeal foramina present.

Description of holotype: (Figs. 1 and 2) All of the bones of the skull are present with the possible exception of the premaxillae which appear to have been eroded away during fossilization. The skull is broad and very deep, with a light encrustation of dermal bone on the frontoparietals (Fig. 3A) and

squamosal, and a very heavy encrustation on the posterior portion of the maxillaries and the posterolateral part of the remaining nasal (Fig. 4M,N). The frontoparietals are thin and emarginate (ragged) medially, thus producing a

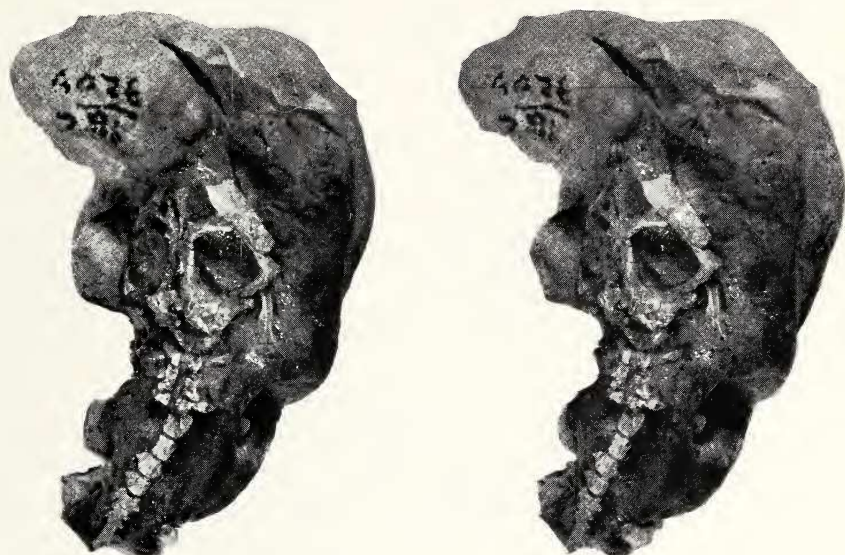


Figure 2. Stereophotograph. Right dorsolateral view of the holotype of *Scaphiopus neuter*. Actual size.

relatively large frontoparietal fontanelle (Fig. 3B). The frontoparietals are narrow and do not show any evidence of a lateral wing-like extension of encrusting dermal bone, nor is there any indication of a frontoparietal boss; both the anterior and posterior openings of the frontoparietal canal can be seen from a dorsal view in the absence of the wing-like extensions (Fig. 3C). The dorsal surface of the prootics is very concave. A large operculum is present. The prootic foramen (for the passage of the trigeminal nerve) is completely enclosed in bone. The dorsal end of the squamosal extends anteroventrally, but it is widely separated from the maxilla. The quadratojugal is absent. The maxillaries are toothed, but the presence of vomerine teeth can not be demonstrated because most of the vomers have been eroded away or are covered with matrix. The palatine bone is absent. The remaining right nasal is in broad contact with the maxilla (Fig. 4N). The maxilla does not possess a shelf-like extension (pterygoid process) posteromedially. The mandible is edentulous. There are nine free (normal) presacral vertebrae (Figs. 1 and 2), all of which appear to be procoelous. Most of the neural arches and the dorsal spines of the vertebrae have been eroded away. The second, third and fourth

vertebrae possess long diapophyses; those of the second vertebra project anterolaterally, the third laterally and the fourth slightly posterolaterally. The diapophyses of vertebrae five through nine have been largely destroyed, but there is some indication that they projected laterally, with the possible exception of those of the ninth which may have been directed slightly anteriorly. The sacral vertebra is completely fused to the coccyx. The sacral diapophyses have

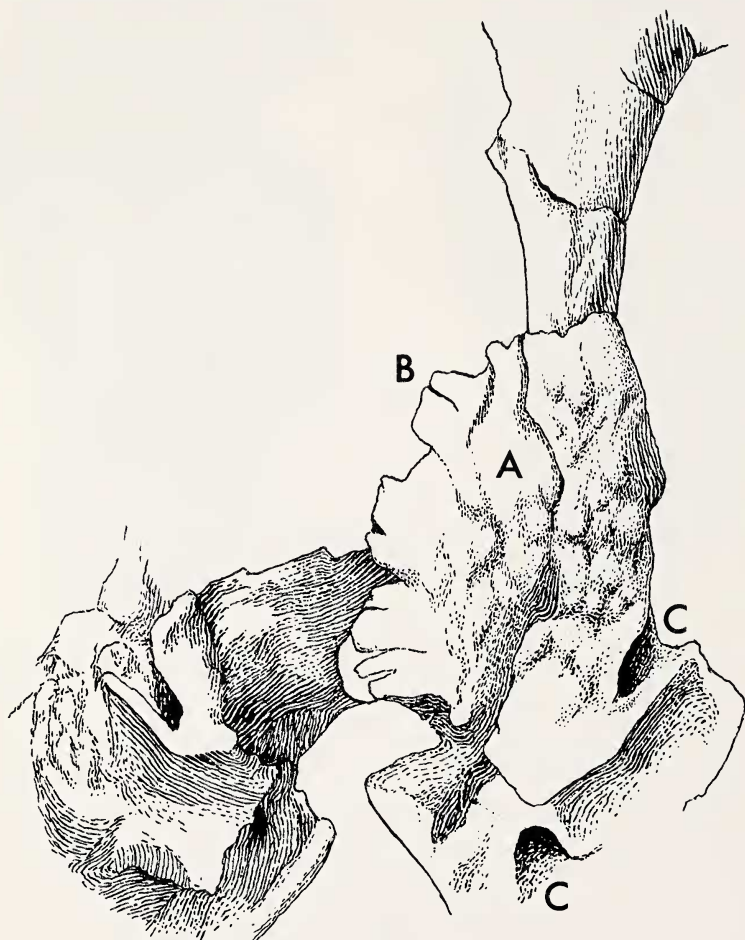


Figure 3. Dorsal view of the frontoparietal region of the holotype of *Scaphiopus neuter*. The right frontoparietal is nearly complete, while the left has largely been eroded away. A. Region of encrusting dermal bone. B. Natural emarginations of frontoparietal bone bordering the frontoparietal fontanelle. C. Anterior and posterior openings of the frontoparietal canal. Scale equals 5 mm.

been almost completely destroyed but the size of their proximal remnants and the position of the intersacral-coccygeal foramen indicate that they were greatly dilated. The postsacral webbing appears to have been extensive; this is

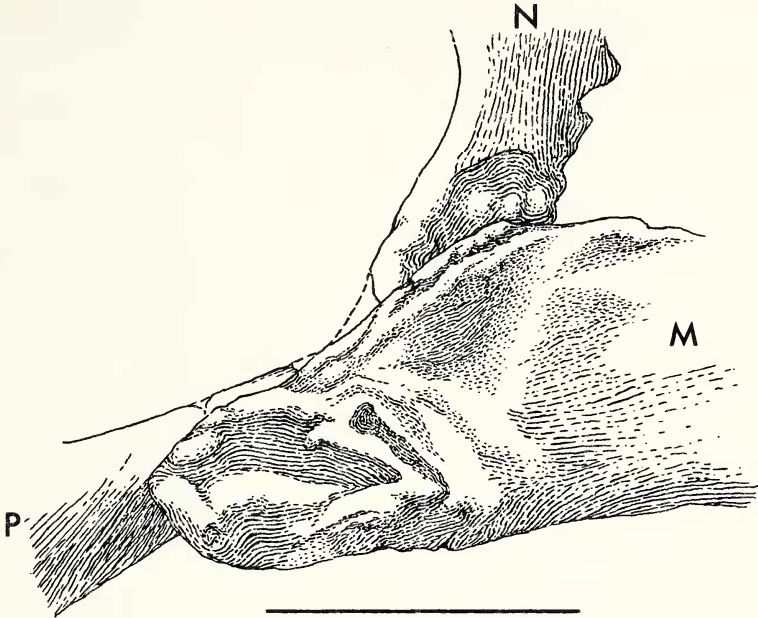


Figure 4. Lateral view of the right maxilla (M), nasal (N) and pterygoid (P) of the holotype of *Scaphiopus neuter*. Note the heavy layer of encrusting dermal bone on the maxilla and nasal. Scale equals 5 mm.

suggested by the length of the lateral remnants and the presence of two postsacral coccygeal foramina. Only the more proximal portion of the coccyx remains; it possesses a relatively low, rounded dorsal crest. The pectoral girdle appears to be arciferous (Fig. 5); the remaining left clavicle is robust and strongly arched anteriorly. The sternal style does not appear to be present in the matrix which may indicate that it was cartilaginous. Both the scapula and the suprascapula are heavy elements. The exposed distal portion of the left humerus possesses a well developed medial epicondyle and a very prominent, anteriorly directed crest. There is a moderately deep depression on the inner surface of the humerus, proximal to the medial epicondyle. The pelvis is represented by both ilia (the proximal end of both of the ilial shafts is missing) and the anterodorsal portions of the ischia (Fig. 6). The ilial shaft is very robust and nearly round in cross-section; the dorsal crest, if present, is represented by only a thin line on the inner aspect of the shaft. Anterior to the acetabular fossa on the ilial shaft is a shallow depression. The dorsal protuber-

ance is extremely large and almost completely occupies the region of the supra-acetabular depression. There appears to be no indication of a dorsal prominence. The acetabular fossa is relatively shallow and the dorsal and anterior parts of the acetabular ridge are very low. The ventral portion of the acetabular ridge is moderately well developed in association with the extremely concave sub-acetabular expansion. The posterior part of the acetabular ridge,

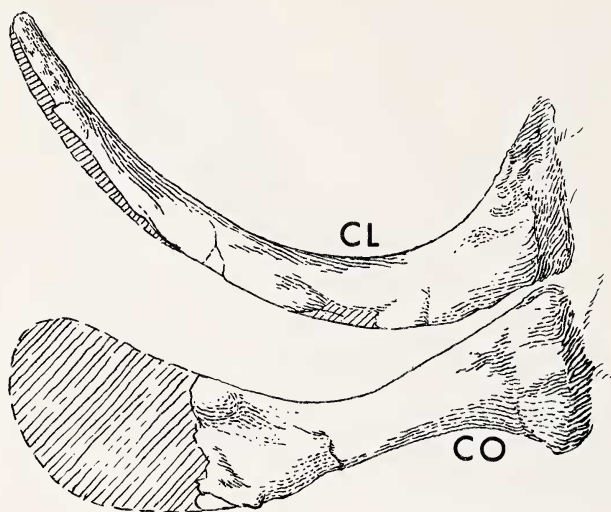


Figure 5. Ventral view of the left clavicle (CL) and coracoid (CO) of the holotype of *Scaphiopus neuter*. Scale equals 5 mm.

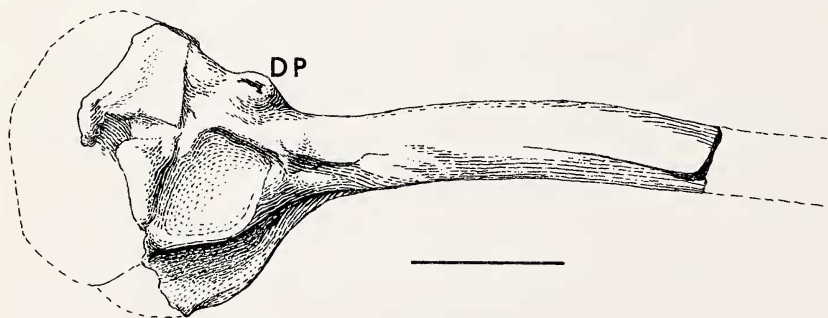


Figure 6. Lateral view of the right pelvis of the holotype of *Scaphiopus neuter*. Note the large dorsal protuberance (DP) on the ilium. Scale equals 5 mm.

situated on the ischium, appears to be well developed. The posterior ischial depression is very deep. The exposed proximal portion of the left femur exhibits a well developed, sharp, posteriorly directed, trochanter ridge. The distal limb elements (including both the hands and feet) are not preserved.

Measurements of holotype (in millimeters): Total head and body length, 85; length of skull from tip of snout to occipital condyles, 24; width of skull between maxillae (posterior extremes), 27; depth of skull from level of frontoparietals to distal tip of quadrate, 12; depth of the deepest part of the body of the ilium, 9. The above measurements are only approximations because of the incompleteness of many of the bones.

Skeletal variation in Recent members of Pelobates and the Scaphiopus-Spea complex: Numerous examples of most of the presently recognized Recent species in the Pelobatinae were examined (with the exception of *Pelobates syriacus*, *P. transcausicus*, and *P. varaldii*) to more accurately determine the intrageneric relationships of *Scaphiopus neuter* (see specimens examined, below). Some of the information on variation has an important bearing on the familial assignment of the fossil as well.

Pasteur (1958) erected the genus *Pseudopelobates* for the species *transcausicus* (previously considered a member of *Pelobates*) on the basis of the following characters: four dorsal vertebrae with very long diapophyses perpendicular to the axis of the vertebral column, and the atlas fused to the first dorsal vertebra. Variability of these same characters in both the Megophryinae and the Pelobatinae (Ramaswami, 1935: 66; Zweifel, 1956; also see following discussion) leads me to consider *Pseudopelobates* a synonym of *Pelobates*. Basoglu and Zaloglu (1964) also consider *transcausicus* to be a member of *Pelobates*. The fact that the characters used by Pasteur are considerably fewer in number and not of the same level of change (e.g., change in length of element versus loss of an element) as those used by Zweifel (pp. 24-5, table 1) to characterize *Pelobates*, *Macropelobates*, *Scaphiopus*, *Spea* and *Neoscaphiopus* (the latter three taxa were considered subgenera) further supports this synonymy.

Classically, the Pelobatidae² were considered to have the usual anuran presacral vertebral number of eight; however, recent studies (with the exception of Adolphi's early contribution in 1895) have indicated considerable variation in the family that encompasses seven to nine vertebrae. Tihen (1960) presented new data and summarized all published information on vertebral variation in Recent and fossil members of the family. His paper clearly shows that any discussion on the number of presacral vertebrae must consider the following points: (1) what are the numbers of the vertebrae (particularly that of the sacrum which is used as the primary reference point in the vertebral sequence), (2) what is the amount of postsacral involvement (postsacral webbing) in the formation of the sacrum, and (3) what is the degree of both

²See Myers and Leviton (1962) for discussion of family name.

pre- and postsacral fusions with the sacrum? The definitive coccyx is formed by the fusion of caudal vertebrae (four in *Megophrys*, Griffiths, 1963). Tihen concluded from his survey that all fusions of the last presacral vertebra with the sacrum in the *Scaphiopus-Spea* group involved the eighth (last presacral) and ninth (sacral) vertebrae. He disagreed with Ritland's (1955) interpretation that the ninth (last presacral) and tenth (sacral—usually the first postsacral vertebral segment embryologically) were fused in the holotype of the extinct *Neoscaphiopus noblei*. The nine presacral vertebrae exhibited by *Scaphiopus neuter* and a Recent specimen of *Scaphiopus intermontanus* (S 2925) strongly suggest that a reconsideration of Ritland's interpretation is in order. Tihen added further support to Chrapliwy's (1956) and Zweifel's (1956) contention that there was a greater degree of vertebral variation (fusion of vertebrae, number of vertebrae, and degree of postsacral webbing) in the Pliocene progenitors of the *Scaphiopus-Spea* complex than there is in their descendent forms. Furthermore, he visualized the variation as normal and as being more markedly reduced in living members of the *Scaphiopus* evolutionary line than in the *Spea* group. Since Tihen's work, Holman (1963) has reported on the fusion of the last presacral vertebra (presumably the eighth) to the sacrum (both were symmetrical in form and their fusion) in a specimen of *Scaphiopus holbrookii*. His total sample consisted of *Pelobates fuscus* subsp. (2), *Scaphiopus bombifrons* (2), *Scaphiopus couchii* (1), *Scaphiopus hammondii* (12), and *S. holbrookii* subsp. (19). Estes and Tihen (1964) referred three fragmentary sacrococcyges from the Early Pliocene Valentine Formation of Nebraska to *Scaphiopus alexanderi*. Although the unique holotype of *S. alexanderi* exhibits fused eighth (last presacral) and ninth (sacrum) vertebrae, the Valentine material does not. In those Recent species that I have studied (see list of specimens examined, below) there is the following variation: in two out of the 89 *S. couchii* the eighth presacral is fused to the sacrum (symmetrical vertebral form and fusion); in one out of the 20 *S. hammondii* (already referred to by Zweifel, 1956: 27) the eighth is fused to the sacrum (symmetrical vertebral form and fusion); in one out of the 34 *S. bombifrons* the eighth is fused to the sacrum (symmetrical in vertebral form, but only partially fused along one sacral diapophysis); in one out of four *S. intermontanus* there is an extra presacral vertebra (ninth) which is fused to the sacrum (symmetrical in vertebral form and fusion). The first and second presacral vertebrae are also completely fused to each other in a single specimen of *S. couchii* (no other vertebral irregularities noted).

Other vertebral variation that was studied in the skeletal material (information from X-ray plates was not used) involved the degree of postsacral webbing, the size of the postsacral nerve foramina, and the shape of the sacral cotyle. The figured examples (*Scaphiopus hammondii*, A-D, and *Scaphiopus bombifrons*, E-G) given by Zweifel (1956: 29, fig. 19A-G; reproduced here as Fig. 7) were used to categorize the variation in postsacral webbing. Table 1 summarizes the information that I have obtained; the nearly random distribu-

tion indicates that the degree of webbing cannot be used to characterize the *Scaphiopus* or *Spea* groups of species.

The size of the postsacral foramen was subjectively delimited as either small or large. *Pelobates fuscus* subsp. (one specimen examined) had a much

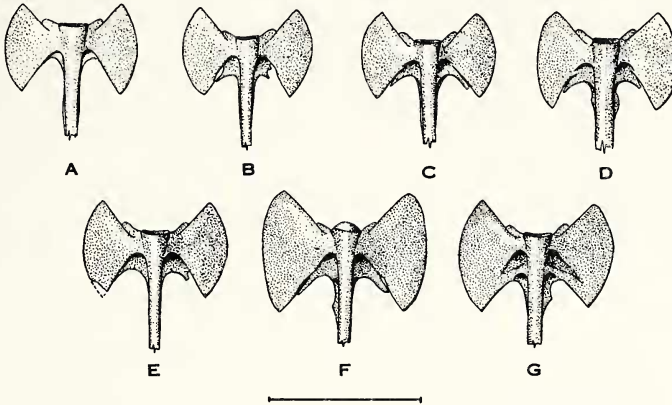


Figure 7. Ventral view of sacral vertebrae, from Zweifel, 1956. A-D. *Scaphiopus hammondii*, Mariposa County, California. E-G. *Scaphiopus bombifrons*, Wyoming. Scale equals 10 mm.

TABLE 1
VARIATION IN POSTSACRAL WEBBING¹

categories	<i>hammondii</i>				<i>bombifrons</i>		
taxa (specimens examined)	A	B	C	D	E	F	G
<i>Pelobates cultripes</i> (3)	3						
<i>Pelobates fuscus</i> (1)							1
<i>Scaphiopus h. holbrookii</i> (18)	15	2			1		
<i>Scaphiopus h. hurterii</i> (2)	2						
<i>Scaphiopus couchii</i> (7)	3				3		1
<i>Scaphiopus intermontanus</i> (5)		1		1		3	
<i>Scaphiopus bombifrons</i> (33)	5	8	2	3	8	4	3
<i>Scaphiopus hammondii</i> (16)	4	5	1		4	2	
total	32	16	3	4	16	9	5

¹Categories of variation, A-G, after Zweifel (1956). See Fig. 7.

larger one. *Scaphiopus h. holbrookii* and *Scaphiopus holbrookii hurterii* had small foraminae, while all *Scaphiopus couchii*, *Scaphiopus intermontanus* and *Scaphiopus hammondii*, and most *Scaphiopus bombifrons* had a large aperture. Only two *S. bombifrons* (33 individuals examined) exhibited a small foramen. A second, more distal, and usually much smaller, postsacral foramen is present in all those specimens that possess more extensive postsacral webbing. Beddard (1907a,b) proposed that the sacrum proper is formed from two vertebrae in *Pelobates* and one in *Scaphiopus*. Apparently, he based his conclusion on the points of exit of the spinal nerves from the vertebral column in the region of the sacrum; I have not been able to duplicate his observations on the material that I have examined.

The cotyle was round in outline in all of the *Pelobates* examined, while all *Scaphiopus h. holbrookii*, *Scaphiopus holbrookii hurterii*, and *Scaphiopus couchii* exhibited an oval depression. In *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii* the cotyle was extremely variable in shape. There was an equal tendency in these species toward roundness or ovalness, and there was no suggestion of sexual or ontogenetic change.

In many different groups of anurans, the proximal end of the columella articulates with a calcified cartilaginous element, the operculum (following Eiselt's terminology, 1942), which is located within the membranous covering of the *fenestra ovalis*. The calcified element is extremely variable intertaxonomically, in size and shape and its attachment to the *M. opercularis*. Functionally, Eiselt considered the columello-operculum-*M. opercularis* as the "Vibrationsleitungsorgan." In dermestid beetle prepared skeletons of the pelobatines that I have studied (those with the membrane of the *fenestra ovalis* still intact), the operculum is either present or absent. I have considered the element to be present when the membrane was opaque (whitish in appearance and of a typical sesamoid composition) and absent when the membrane was transparent (nearly so in the dried state). Even in the latter condition, there may be a small amount of calcification, as indicated by clearing and staining preserved specimens with Alizarin red-S, in spite of the fact that the membrane is transparent in dermestid beetle prepared material of the same species. This may account for the discrepancies between Eiselt's data on the occurrence of the operculum in fluid preserved pelobatids and that presented here. By my method of determination, the operculum is absent in all *Pelobates cultripes*, *Pelobates fuscus* subsp., *Scaphiopus h. holbrookii* and *Scaphiopus holbrookii hurterii*, and present in all *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii*. The operculum was present (62.5%) or absent (37.5%) in *Scaphiopus couchii*; when present it was extremely small and in one specimen it was absent on one side.

One of the most conspicuous features of the skull of pelobatines is the degree of development and distribution of encrusting dermal bone. Only its distribution on the frontoparietal, posterior portion of the maxillae, and posteroventral section of the nasals is considered here because of its presence on

these areas in *Scaphiopus neuter*. For the purpose of this discussion, the degree of development of the encrustation has been categorized as extensive, moderate, limited, or absent. In *Pelobates*, *Scaphiopus h. holbrookii*, *Scaphiopus holbrookii hurterii* and *Scaphiopus couchii* the frontoparietal is extensively covered; there may be subtle differences between the two genera, however, they are difficult to quantify. The dermal encrustation is absent (*sensu stricto*) in *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii* (see following discussion of the frontoparietal boss). The encrustation on the maxillae and nasals was extensive in *Pelobates*, limited to extensive in *S. h. holbrookii*, *S. h. hurterii* and *S. couchii* (modally extensive), and absent in *S. intermontanus*, *S. bombifrons* and *S. hammondii*. A single adult male *S. hammondii* (S 2384) from El Toro, Orange County, California, exhibited a limited degree of encrustation; in other specimens from the same locality, the encrustation was absent.

The trend toward reduction of encrusting dermal bone in the Pelobatinae has a positively correlated, and thus complementary, trend in the degree of contact between the frontoparietal and the squamosal and the squamosal and the maxilla. In *Pelobates cultripes* the frontoparietal-squamosal and the squamosal-maxilla contacts are extensive. In *Pelobates fuscus* subsp. the frontoparietal and the squamosal are not joined, and the squamosal-maxilla union is slightly reduced in width; the frontoparietal-squamosal union is also interrupted in all *Scaphiopus*. In *Scaphiopus couchii* the width of the zone of contact between the squamosal and the maxilla is narrower than that in *Scaphiopus h. holbrookii* and *Scaphiopus holbrookii hurterii*. In *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii* the squamosal and maxilla are widely separated from each other. The squamosal in these three species is greatly reduced in size and does not exhibit any obvious degree of encrustation.

As has been recognized for many years in the pelobatines, the dorsal enlargement of the frontoparietal bone (boss) is characteristic of only *Scaphiopus intermontanus* and *Scaphiopus bombifrons*. A well developed boss may give the appearance of extra-dermal bone. Hughes (1965) used the thickness of the boss as an index to the degree of hybridization in a mixed breeding population of *Scaphiopus hammondii* and *S. bombifrons* from Lubbock County, Texas. My observations indicate that there is considerable ontogenetic change in the size of the boss; absent or only poorly developed in the small *S. intermontanus* and *S. bombifrons* to well developed in large individuals. Because Hughes did not take into account the parameter of growth, his data on hybridization must be considered inconclusive. My observations do not indicate any sexual differences in the degree of development of the boss. In comparing individuals of the same size, the boss of *S. bombifrons* usually appeared to be larger than that of *S. intermontanus*.

The presence of the frontoparietal fontanelle is positively correlated with the absence of encrusting dermal bone in pelobatines; the fontanelle is present

in *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii*, and absent in all other species. The formation of the fontanelle appears to be an extension of the evolutionary trend toward reduction of encrusting bone in the subfamily (I have assumed that the trend has proceeded from a massive type of skull, as exhibited by *Pelobates cultripes*, to the delicate form of *S. hammondii*). From my field experience with *Scaphiopus couchii* (dermal encrustation present, fontanelle absent) and *S. hammondii* (dermal encrustation absent, fontanelle present) in the southwestern United States, and from a survey of the literature, this trend in morphology does not appear to be correlated with any obvious change in the substrate and burrowing habits of the species as one might suspect. The smallest fontanelle appears to be exhibited by *S. intermontanus* and the largest by *S. hammondii* (comparing individuals of approximately the same size). The fact that the development of the frontoparietal boss obscures the overall size of the fontanelle makes this very difficult to observe, however.

In *Pelobates* and *Scaphiopus h. holbrookii*, *Scaphiopus holbrookii hurterii* and *Scaphiopus couchii*, a slightly to moderately well developed pterygoid process of the maxilla is present (Table 2). This process is a posteromedial projection that borders the lateral surface of the pterygoid bone, immediately anterior to the plane of squamosal-maxilla contact. In *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii* the process is almost always absent (Table 2). The marked similarity of Tables 2 and 3 appears to be coincidental.

TABLE 2
VARIATION IN THE LENGTH OF THE
PTERYGOID PROCESS OF THE MAXILLA

variation	absent	short	long
taxa (specimens examined)			
<i>Pelobates cultripes</i> (3)		3	
<i>Pelobates fuscus</i> (1)		1	
<i>Scaphiopus h. holbrookii</i> (18)		12	6
<i>Scaphiopus h. hurterii</i> (2)		1	1
<i>Scaphiopus couchii</i> (7)			7
<i>Scaphiopus intermontanus</i> (4)	4		
<i>Scaphiopus bombifrons</i> (34)	32	2	
<i>Scaphiopus hammondii</i> (16)	13	3	

TABLE 3
VARIATION IN THE SIZE OF THE PALATINE BONE

variation taxa (specimens examined)	absent	small	large
<i>Pelobates cultripes</i> (3)		3	
<i>Pelobates fuscus</i> (1)		1	
<i>Scaphiopus h. holbrookii</i> (18)		2	16
<i>Scaphiopus h. hurterii</i> (2)		1	1
<i>Scaphiopus couchii</i> (7)			7
<i>Scaphiopus intermontanus</i> (4)	4		
<i>Scaphiopus bombifrons</i> (34)	32	2	
<i>Scaphiopus hammondii</i> (16)	13	3	

The optic, oculomotor and trigeminal nerves enter the posterior quadrant of the ocular orbit from the cranial vault from anterior to posterior, respectively. In *Pelobates* and the *Scaphiopus-Spea* group the optic foramen (or its bony emargination) is extremely large, while the oculomotor foramen is correspondingly small (not always discernible as a discrete aperture). The prootic foramen, for the passage of the trigeminal nerve, is highly variable in the degree of encirclement by bone; this variation involves a well defined morphogenetic trend. In *Scaphiopus h. holbrookii* and *Scaphiopus holbrookii hurterii* the prootic foramen is widely emarginate anteriorly; absence or near absence of an emargination in *Pelobates* suggests an even earlier stage of evolution of the prootic foramen. *Scaphiopus couchii* exhibits a slightly narrower emargination than that characteristic of *S. holbrookii*, but usually wider than the condition exemplified by *Scaphiopus intermontanus*, *Scaphiopus bombifrons* or *Scaphiopus hammondii*. The latter three species indicate the culmination of this morphogenetic trend (n = narrowly emarginate; s = split-like emargination; c = prootic foramen completely encircled by bone); *S. intermontanus* (n = 60%, s = 20%, c = 20%), *S. bombifrons* (n = 17.7, s = 29.4, c = 52.9), *S. hammondii* (n = 46.7, s = 13.3, c = 40). No sexual dimorphism and little ontogenetic change in this character was noted.

As Zweifel (1956: 38, fig. 24) has already pointed out, one of the most peculiar morphogenetic trends in *Pelobates* and *Scaphiopus* is the reduction of the palatine (as a ridge of bone fused to the maxilla) and its replacement by a process of vomer. In pelobatines, the palatine bone appears to be fused to the maxilla by the time of metamorphosis; a recently transformed *Scaphiopus h.*

holbrookii (S 2494) of 12 mm. snout to vent length did not have a center of palatine ossification separate from that of the maxilla. The process of the vomer is usually absent in *Pelobates* (if indicated it is very small and widely separated from the palatine), while in all members of the genus *Scaphiopus* it is extremely long, contacts the palatine (when present), and closely approaches the medial margin of the inner shelf of the maxilla. The length of the process of the vomer in *Scaphiopus* appears to be relatively constant from species to species, however, its replacement of the palatine is more obviously seen in its increasing depth (this contradicts that suggested by Zweifel, 1956; see his fig. 24). In *Pelobates*, the palatine is narrow, and very long and shallow, relative to that in *Scaphiopus holbrookii*. In *S. holbrookii* and *Scaphiopus couchii* the palatine is very wide and deep and only slightly shorter than that seen in *Pelobates* (this differs from that stated by Zweifel, 1956; table 1). The initial stages of palatine reduction appear to be in its width, more specifically along the anterior zone of palatine-maxilla fusion (e.g., compare *S. holbrookii* with *S. couchii*). It is only in *Scaphiopus intermontanus*, *Scaphiopus bombifrons* and *Scaphiopus hammondii* that the depth of the process is affected. Table 3 graphically presents this trend.

TABLE 4
DEGREE OF DEVELOPMENT OF THE DORSAL PROTUBERANCE
OF THE ILIUM

variation	absent	small	moderate	large
taxa (specimens examined)				
<i>Pelobates cultripes</i> (3)	3			
<i>Pelobates fuscus</i> (1)	1			
<i>Scaphiopus h. holbrookii</i> (18)	5	9	4	
<i>Scaphiopus h. hurterii</i> (1)				1
<i>Scaphiopus couchii</i> (7)	3	3	1	
<i>Scaphiopus intermontanus</i> (5)	3	2		
<i>Scaphiopus bombifrons</i> (34)	11	17	6	
<i>Scaphiopus hammondii</i> (15)	3	6	5	1

The dorsal protuberance of the ilium (following the terminology proposed by Estes and Tihen, 1964: 457) is usually absent or only slightly developed in pelobatines (Table 4). Because of the difficulty in accurately measuring the size of the protuberance, the degree of development, relative to its protusion

above the surface and the dorsal border of the supra-acetabular expansion, it was subjectively categorized as absent, small, moderate or large (see Table 4). The degree of development of the protuberance is clearly not sexually dimorphic, nor does there appear to be any ontogenetic relationship; the latter finding differs from that suggested by Estes and Tihen (1964). The information presented in Table 4 does not suggest any interspecific differences in *Scaphiopus*. The absence of the dorsal protuberance in the four *Pelobates* examined agrees with the observations of Estes and Tihen (1964: 459).

Taxonomic position of Scaphiopus neuter: The condition of sacrococcygeal fusion, markedly dilated sacral diapophyses, procoelous vertebrae and an arciferal pectoral girdle makes the assignment of *Scaphiopus neuter* to the family Pelobatidae relatively certain. The presence of a free coccyx in the following modern families removes them from being considered closely related to the fossil: Ascaphidae, Discoglossidae, Rhinophrynidae, Pelodytidae, Leptodactylidae (including Pseudinae and Rhinodermatinae), Bufonidae, Hylidae, Centrolenidae, Dendrobatidae and Sooglossidae.

The coccyx is not fused to the sacrum in some members of the Pipidae and Atelopodidae, and it is usually free in the Microhylidae, Phrynomeridae, Ranidae, Rhacophoridae and megophryine pelobatids (intraspecifically variable in *Megophrys*). Griffiths (1963: 271) recently defined the Pelobatinae on the basis of their anchylosed sacrococcyx, whereas in the Megophryinae these elements were not considered to be fused together. The sacrum and the coccyx are reported to be fused in *Megophrys nasuta* (Beddard, 1907a; Boulenger, 1908) and occasionally fused in *Megophrys major* (Boulenger, 1908; Ramaswami, 1935). Zweifel (1956: fig. 5) also showed a diagram of a *Megophrys* (c.f.) *monticola* with a fused sacrococcyx; it must be pointed out that *M. nasuta* and *M. monticola* have recently been considered conspecific (Inger, 1954). In the Megophryinae, this variation appears to be limited only to the genus *Megophrys*, and within it to only two or three species out of approximately 24 that are currently recognized. In the Pelobatinae, *Pelobates cultripes* does not exhibit a completely anchylosed sacrococcyx in the sense that it occurs in *Pelobates fuscus* and in the genus *Scaphiopus*. The union of the sacrococcyx in *P. cultripes* is usually indicated by a thin, ventral suture, although the two elements can only be separated with difficulty in subadult-adult animals. The sacrococcyx union in *P. cultripes* seems to represent an evolutionary stage intermediate between the usual free condition in the Megophryinae and the fused state in the Pelobatinae.

The presence of cylindrical or but slightly expanded, sacral diapophyses in the following families also excludes them from being considered closely allied to *Scaphiopus neuter*: Ascaphidae, Leptodactylidae, Dendrobatidae, Ranidae and Rhacophoridae. The presence of procoelous presacral vertebrae in the fossil suggests that it does not belong to the Ascaphidae (amphicoelous), Discoglossidae, Pipidae or Rhinophrynidae (either opisthocelous or biconcave), Phrynomeridae (diplasiocoelous), or Ranidae, Rhacophoridae or Hy-

peroliidae (almost always diplasiocoelous). Boulenger (1908) found some evidence of both procoely and opisthocoely in the genus *Megalophrys* (now included in *Megophrys*) and Griffiths (1963) noted free intervertebral discs in a four-year-old adult *Megophrys major* (family Pelobatidae). The apparent presence of an arciferal pectoral girdle in the fossil also indicates that it should not be considered a member of the Microhylidae, Ranidae, Rhacophoridae or Hyperoliidae. The tendency towards the development of a firmisternal pectoral girdle in the Atelopodidae and Dendrobatidae, and the firmisternal or partly arciferal girdle of the Pipidae removes them from possible consideration as well. The frequent reduction of the number of presacral vertebrae in the former two families even further removes them from consideration. The only family that completely agrees with those characters noted above for the fossil is the Pelobatidae², more specifically the subfamily Pelobatinae. The fossil does not exhibit any characteristics that contradict its placement in the Pelobatidae.

Beddard (1907b) stated that the presence of two cricoid cartilages, the more or less rudimentary condition of the metatarsal tubercle, the less completely webbed hind toes, the presence of a glandular patch on the thighs (absent in *Megophrys feae*, Beddard, 1911), and the absence of the anterior hyoidean cornua can be used to distinguish the Oriental pelobatids (= Megophryinae) from *Pelobates* and presumably *Scaphiopus* (= Pelobatinae). This dichotomy follows the lines of megophryine-pelobatine evolution recognized here, but unfortunately these particular characters cannot be applied to fossil material.

Recent papers by Griffiths (1963: 258, 279) and Tihen (1965) have strongly emphasized the importance of the number of free presacral vertebrae (nine, or less) in delimiting ordinal-subordinal phylogeny and evolutionary trends in the Anura. Neither author mentioned the fact that discoglossids have eight or nine vertebrae (although the latter number only rarely) and that seven to nine vertebrae occur in the Pelobatidae (see previous discussion). This degree of variation in "more primitive" frogs suggests that the number of vertebrae be considered of less paleotelic weight (*sensu* Camp, 1923) than that accorded to it by Griffiths and Tihen. In my opinion, the presence of nine (normal) presacral vertebrae in *Scaphiopus neuter*, does not dictate that it should be placed in the notobatrachid-ascaphid evolutionary line as outlined by Griffiths and Tihen.

The general form of the pelvic girdle (see Zweifel, 1956: fig. 7), the fused sacrococcyx, the reduced dermal encrustation on the skull and the presence of a frontoparietal fontanelle, and the form, length and direction of the diapophyses of the presacral vertebrae (see Zweifel, 1956: figs. 5, 14) strongly indicates that the fossil is a member of the subfamily Pelobatinae. I consider the Pelobatinae to include only the Recent genera *Pelobates* (including *Pseudopelobates* as previously discussed) and *Scaphiopus* (and *Spea*). The extinct genera, *Archaeopelobates* Kuhn, *Eopelobates* Parker, *Macropelobates* Noble, *Miopelobates* Wettstein-Westersheimb, *Palaeopelobates* Kuhn, and *Pelobatinopsis* Kuhn, all appear to be more closely associated with the megophryine

evolutionary line in the family rather than with the Pelobatinae (Wettstein-Westersheimb, 1955; Kuhn, 1962; Griffiths, 1963: 271). The Upper Jurassic genus *Stremmia* Nopsca, placed in the Pelobatidae by Reig (1958), is probably not an amphibian (Hecht, 1960). The Lower Cretaceous pelobatids [?] from Israel (Nevo, 1956) have not been studied in sufficient detail to be considered here.

Both Noble (1924) and Zweifel (1956) considered the Oligocene *Macropelobates* to be more closely related to *Pelobates* and *Scaphiopus* than to the Megophryinae. The free coccyx, form of the greatly expanded sacral diapophyses, length and angle of the diapophyses of the more caudal presacral vertebrae, and the shape and relative size of the ischium and the ilium are characteristics that *Macropelobates* shares with many megophryine species of *Eopelobates* and *Megophrys*. The presence of an apparently all bony pubis and a large prehallux (with a digging tubercle) in *Macropelobates* could indicate that the genus is near the point of divergence of the megophryine and pelobatine evolutionary lines. However, the Oligocene time of origin for *Scaphiopus* and *Spea*, as discussed later, rules against this thesis.

The distribution of the quadratojugal in the Pelobatinae (present in *Pelobates*, absent in *Scaphiopus*) clearly indicates an early point of evolutionary divergence within the subfamily as it is now recognized. The length of the sacrococcyx (less than six presacral vertebrae in *Pelobates*, greater than seven in *Scaphiopus*) and the width of the sacral diapophyses (equal to the length of four presacral vertebrae in *Pelobates*, two in *Scaphiopus*) are slightly variable characters, but they too support the recognition of the point of divergence based on the distribution of the quadratojugal. The size and form of the palatine, the presence of a bony or cartilaginous sternal style, and the angle of the diapophyses of vertebrae five through eight to the axis of the vertebral column (see Zweifel, 1956: table 1) are considerably more variable (see previous discussion, above), and while they also suggest the dichotomy, they cannot be considered absolute indicators of it. The absence of the quadratojugal, the probable cartilaginous sternal style, and the only slightly angulated diapophyses of vertebrae five through nine in the fossil species *neuter* strongly supports its placement in the genus *Scaphiopus*. Griffiths' (1963: 271) statement that all pelobatids have an ossified sternal apparatus is incorrect (see Ramaswami, 1935: 67, and Zweifel, 1956: 24).

The presence of two natural groups of species within the genus *Scaphiopus* has been recognized for many years, and their taxonomic status has received considerable debate. The utility of the generic category is without question and yet the objective reality of the taxon has received ever increasing discussion. In an attempt to form a more consistent definition of the generic category, Inger (1954, 1958) has suggested that genera, particularly in amphibians, should be defined on the basis of their adaptive features ("genetics, developmental mechanics, behavior, ecology, etc.") rather than, for example, the more classical morphotype approach. From my own studies on

gekkonid lizards, and from similar investigations on plethodontid salamanders (David B. Wake, pers. communication) it appears that an adaptive definition by itself has no greater advantage over any other criterion that is founded on evolutionary principles. From the gekko and salamander studies it has become very obvious that adaptive parallelisms are much more common than formerly realized and thereby rules against the adaptive criterion being the only character used to define a genus. It is obvious that the more information we accumulate on a group of related species, particularly from fossil forms, the less clear the generic limits will be. It is my opinion that to continue to argue whether the *Scaphiopus* and *Spea* groups are accorded generic or subgeneric rank is without merit, as all higher taxonomic categories are entirely man-made assemblages and therefore of a wholly arbitrary nature (Simpson, 1961). My choice of considering *Spea* a subgenus, rather than a genus, is completely arbitrary. Table 5 is a summary of the major characters, both morphological and "adaptive" that distinguish the *Scaphiopus* and *Spea* evolutionary lines (see previous discussion of osteological variation). The hybridization experiments that have thus far been carried out by A. Blair (1947), Littlejohn (1959), and Wasserman (1957; 1958) also support the recognition of this dichotomy.

The lack of contact between the maxilla and squamosal, the completely bone encircled prootic foramen, the presence of a frontoparietal fontanelle, the absence of a pterygoid process of the maxilla, and the absence of a palatine bone suggest that *Scaphiopus neuter* is closely related to the *Spea* evolutionary line (see Table 5). In contrast to this inferred relationship, the presence of encrusting dermal bone on the skull (although relatively limited) and the presence of an operculum points to an affinity between *S. neuter* and the *Scaphiopus* line. The head and body size of *S. neuter* may also be indicative of a relationship with *Scaphiopus* (see Estes and Tihen, 1964). As has already been discussed above, the number of vertebrae (including presacral-sacral fusions), the degree of postsacral webbing, the size of the postsacral nerve foramina, and the shape of the sacral cotyle are considerably more variable than previously realized, and therefore do not appear to be useful in referring *S. neuter* to either the *Scaphiopus* or *Spea* complexes. Without assigning paleotelic values to the above noted characters, the relationships of *S. neuter* appear to lie within the *Spea* line of divergence; however, those *Scaphiopus* characteristics that it exhibits indicate that it is near the point of divergence between the two subgenera. The Lower Miocene age of *S. neuter* points to at least an Oligocene time of origin for *Scaphiopus* and *Spea*. Figure 8 pictorially represents the proposed relationships.

The presence of a frontoparietal boss in both *Scaphiopus intermontanus* and *Scaphiopus bombifrons* strongly suggests a closer degree of affinity than either species has with *Scaphiopus hammondi*. The relationship between *S. intermontanus* and *S. bombifrons* is also clearly exemplified by their similar breeding calls (W. Blair, 1956; McAlister, 1959). The relatively smaller fronto-

TABLE 5
SUMMARY OF THE DIAGNOSTIC CHARACTERS DISTINGUISHING
SPEA COPE FROM *SCAPHIOPUS* HOLBROOK

<i>Scaphiopus</i> Holbrook	<i>Spea</i> Cope
<i>h. holbrookii</i> Harlan—Pleist.-Recent (incl. <i>albus</i> Garman ¹)	<i>intermontanus</i> (Cope) ⁵ —Recent
<i>h. hurterii</i> Strecker ² —Pleist.-Recent	<i>bombifrons</i> (Cope)—Pleist.-Recent
<i>couchii</i> (Baird)—Pleist.-Recent (incl. <i>rectifrenis</i> Cope ³)	<i>hammondii</i> (Baird)—Recent (incl. <i>multiplicata</i> Cope ⁶)
<i>wardorum</i> Estes and Tihen—Lower Plio. species from Florida— Lower Mio. ⁴	<i>diversa</i> (Taylor)—Upper Plio. (incl. <i>noblei</i> Taylor ⁷)
	<i>pliobatracha</i> (Taylor)—Mid. Plio. (incl. <i>antiquus</i> Taylor ⁸)
	<i>studerii</i> (Taylor)—Mid. Plio.
	<i>alexander</i> (Zweifel)—Lower Plio.
1. maxilla and squamosal in contact	1. maxilla and squamosal not in contact
2. prootic foramen widely emarginate	2. prootic foramen narrowly emarginate
3. metatarsal tubercle sickle-shaped	3. metatarsal tubercle cuneiform
4. frontoparietal fontanelle absent	4. frontoparietal fontanelle present
5. dermal encrustation on skull extensive	5. dermal encrustation on skull absent
6. operculum usually present and large	6. operculum absent
7. pterygoid process of maxilla present	7. pterygoid process of maxilla almost always absent
8. palatine present	8. palatine almost always absent
9. adults large, up to 82 mm. snout to vent length	9. adults of medium size, up to 65 mm. snout to vent length
10. paratoid gland present or indistinct	10. paratoid gland absent
11. vocal sac single or only slightly divided into two compartments ⁹	11. vocal sac completely divided into two compartments ⁹
12. sound of call comes from vocal cords proper and edges of vocal cords ⁹	12. sound of call comes from edges of vocal cords ⁹
13. call not trilled ^{9,10}	13. call trilled ^{9,10}
14. call slightly modulated ⁹	14. call considerably modulated ⁹
15. eggs small, extensive pigmentation, with single indistinct jelly envelope ¹¹	15. eggs large, little pigmentation, two or three jelly envelopes ¹¹
16. tadpoles small, usually less than 30 mm., usually darkly colored ³	16. tadpoles large, up to 50 to 90 mm., seldom darkly colored ³
17. usually occupy more mesic environment ¹²	17. usually occupy more xeric environment

¹*fide* Duellman and Schwartz (1958).

²as a subspecies of *holbrookii*: *fide* W. Blair (1958), Wasserman (1957, 1958).

³*fide* Chrapliwy (1956).

⁴Auffenberg (1956). Presently being studied by J. Alan Holman.

⁵as a species distinct from *hammondii*: *fide* Chrapliwy (1956), W. Blair (1956), McAlister (1959), McCoy (1962).

parietal fontanelle (with ragged margins) and boss in *S. intermontanus* may indicate a more primitive stage of evolution than that shown by *S. bombifrons*. The absence of a boss and the presence of a small frontoparietal fontanelle (with ragged margins) in *Scaphiopus neuter* indicates that it may have been phylogenetically near the point of separation between *S. hammondii* and the closely related *S. intermontanus* and *S. bombifrons*.

Scaphiopus neuter was collected in association with numerous mammals: (Macdonald, 1963): a marsupial (*Peratherium spindleri*), insectivores (*Ocajila makpiyahe*, *Arctoryctes terrenus*), rabbits (*Palaeolagus hypsodus*, *Palaeolagus philoi*), an ischyromyid rodent (*Prosciurus dawsonae*), a heteromyid rodent (*Florentiamys agnewi*), beavers (*Palaeocastor nebrascensis*, *Capatanka cank-peopi*, *Capacikala gradatus*), canids (*Nothocyon roii*, *Sunkahetanka geringen-*

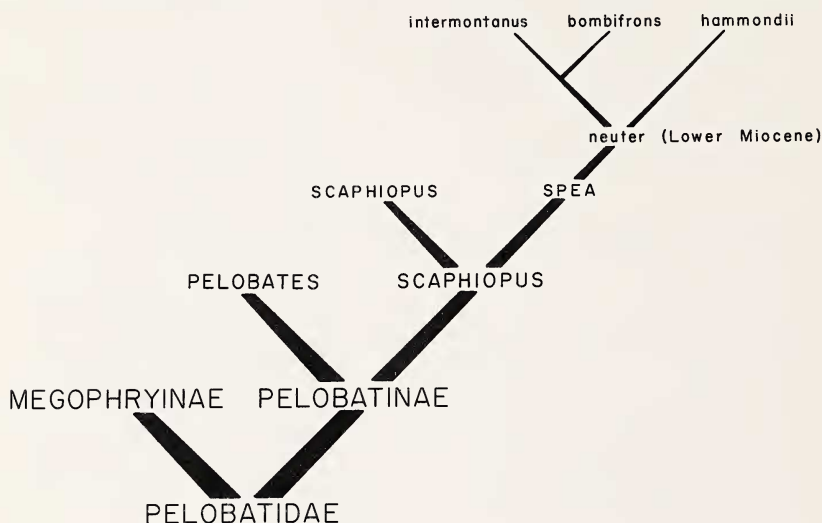


Figure 8. Dendrogram showing the phylogenetic position of *Scaphiopus neuter* within the Pelobatidae.

⁶the few diagnostic characters and the extreme width of the zone of integration does not appear to warrant the further recognition of *multiplicata* (Chrapliwy, 1956; Zweifel, 1956).

⁷my examination of the holotype of *Neoscaphiopus noblei* (KUMVP 6367) confirms Tihen's (1960) reference of that genus and species of the synonymy of *diversa*.

⁸my examination of the holotype of *Scaphiopus antiquus* (KUMVP 1469) confirms Tihen's (1960) reference of that species to the synonymy of *plioatracha*.

⁹*vide* McAlister (1959).

¹⁰*vide* W. Blair (1955, 1956, 1958).

¹¹*vide* Hoyt (1960); not determined for *intermontanus*.

¹²some major exceptions in *couchii*.

sis, *Enhydrocyon crassidens*), horses (*Miohippus* near *equinanus*, *Miohippus equiceps*), a rhinocerotid (*Diceratherium* cf. *gregorii*) and hypertragulids (*Leptomeryx* sp., *Nanotragulus intermedius*). These faunal associates seem to support Zweifel's contention (1956: 41) that the evolution of the *Spea* group may have been correlated with the establishment of a grassland.

SUMMARY

A new species of pelobatid frog, *Scaphiopus neuter*, is described from the Wounded Knee area of Shannon County, South Dakota. It was collected in the Sharps Formation, Arikaree Group, of the Lower Miocene. Numerous skeletons of most of the Recent species of *Pelobates* and *Scaphiopus* were examined to assess the intrageneric relationships of the fossil. The general form of the pelvic girdle, the fused sacrococcyx, the reduced encrusting dermal bone on the skull and the presence of a frontoparietal fontanelle, and the form, length and direction of the diapophyses of the presacral vertebrae strongly indicate that the fossil is a member of the subfamily Pelobatinae and more specifically the genus *Scaphiopus*. The absence of a quadratojugal further supports its placement in *Scaphiopus*. *Scaphiopus neuter* appears to be phylogenetically near the point of divergence of the subgenera *Scaphiopus* and *Spea*. The Lower Miocene age of the fossil indicates that the two subgenera probably originated by the Oligocene.

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gan have kindly read the manuscript and have offered many valuable suggestions.

Skeletal material examined:

Pelobates

cultripes (4 specimens)—JMS 331, S 2629-31 (no locality data).

fuscus subsp. (1 specimen)—S 1226 (Austria).

Scaphiopus

bombifrons (34 specimens)—United States: S 161 (Arizona); S 2265, 2284, 2592-9, 2600-19 (Kansas); S 123, 162-3 (Wyoming).

couchii (13 specimens)—Mexico: S 2415-6 (Coahuila); JMS 738, 740, 754, 776, 785 (Sinaloa); S 2011, 2263 (Sonora); an additional 76 preserved specimens from the collections of the University of Southern California were X-rayed (Baja California, Sinaloa and Sonora). United States: S 2410 (New Mexico); S 156, 1593, 2358 (Texas).

hammondii (including *multiplacatus*) (20 specimens)—Mexico: S 2312-3 (Coahuila); S 964 (Distrito Federal); S 1674 (Durango); S 1171 (Michoacan); S 2218-9 (Oaxaca); S 157 (San Luis Potosi). United States: S 159, 2409 (Arizona); JMS 415, 419, 451-2, S 2384-7 (California); S 2472 (Nevada); S 2406 (New Mexico).

h. holbrookii (20 specimens)—United States: S 158, 968, 1021, 1324, 2494 (Florida); S 974-5 (Georgia); S 1174, 1260-70 (South Carolina); S 2493 (West Virginia).

holbrookii hurterii (2 specimens)—United States: S 794 (no locality data); S 1228 (Texas).

intermontanus (5 specimens)—United States: S 155, 2353, 2868, 2924-5 (Utah).

Fossil material examined:

Scaphiopus antiquus Taylor (1941). Holotype KUMVP 1469. Middle Pliocene. "Edson beds," Ogallala Formation, Sherman County, Kansas.

Scaphiopus diversus Taylor (1942). Holotype KUMVP 6368. Upper Pliocene. Rexroad Formation, Meade County, Kansas.

Scaphiopus cf. *holbrookii*, Auffenberg (1956). Referred material UF 6502, 9896-9 (including material from Florida Geological Survey) and Museum of Comparative Zoology, Harvard University (uncatalogued). Early Miocene. Thomas Farm, Gilchrist County, Florida.

Neoscapthiopus noblei Taylor (1942). Holotype KUMVP 6367. Upper Pliocene. Rexroad Formation, Meade County, Kansas.

Scaphiopus pliobatrachus Taylor (1936). Holotype KUMVP 1430. Referred material KUMVP 1431-6. Middle Pliocene. "Edson beds," Ogallala Formation, Sherman County, Kansas.

Scaphiopus studeri Taylor (1938). Holotype KUMVP 1478. Middle Pliocene. "Rhino Hill Quarry," Logan County, Kansas.

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